$\lvert T_{ii-1}\rvert$	$2\pi/w$
0.2	55.8
0.5	50.7
1.0	48.6
2.0	48.1
3.0	47.9
4.0	47.9
5.0	47.8

fig. 3

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identical phase (within 2% or so). The period and the phase shifts can be very accurately predicted (within 1%) by replacing the network with a three ring whose parameters are given by the averages (average weight ± 0.01 and average delay 10) and using (18) and (19). Similar results were obtained also with larger delays chosen uniformly over [0,50].

Figure Captions

fig. 1: The output of the first neuron in an all-excitatory $n = 4$ and $n = 5$ ring when starting very close to the unstable limit cycle. This can be achieved by letting the corresponding network, with one inhibitory connection, relax to its limit cycle near the bifurcation point, and then suddenly shift the inhibitory connection to excitatory, while introducing a delay of half a period between the corresponding two neurons. Parameter values for the two rings are $T_{ii-1} = 0.3$, $g_i = 1$ and $\tau_i = 7$ for any i. The unique delay in the $n = 4$ (resp. $n = 5$) ring is 21 (resp. 28). Notice that the larger system remains close to its unstable cycle for a longer time.

fig. 2: The stable limit cycle of a $n = 4$ ring with only one inhibitory connection between neurons 4 and 1, represented by the output of each one of the neurons. Parameter values are $|T_{ii-1}| = 0.3$, $g_i = 1$ and $\tau_i = 7$ for any i. The unique delay is $\tau_{14} = 10$. The duration of the transient, from initial random conditions, does not exceed one period.

fig. 3: Table relating the period $2\pi/\omega$ of the stable limit cycle of a 3 neuron ring with one inhibitory connection to the common magnitude magnitude of the weights $|T_{ii-1}|$. Other parameter values are $\tau_i = 7$ and $g_i = 1$ for $i = 1,2,3$. There is a unique delay $\tau_{13} = 10$. The period, as estimated theoretically from the linear approximation (19) near the bifurcation point equals 55.5. The theoretical estimate for the high gain (or high $|T_{ii-1}|$) limit (22) equals 47.7. Both estimates are in good agreement with the observed period.

fig. 4: (a) A five-neuron ring. (b) An example of a three layer network used in the simulations: the weights from layer 1 to 2 and from layer 2 to 3 are positive, and those from layer 3 to layer 1 are negative.

fig. 5: The stable limit cycle of a three layer network, with 10 neurons per layer. All weights from layer 1 to 2 and from layer 2 to 3 are positive and generated from a uniform distribution over the interval [0,0.02]. The weights from layer 3 to 1 are all negative and generated from a uniform distribution over [-0.02,0]. For every i, we have $g_i = 1$ and $\tau_i = 7$. Each connection has a delay τ_{ij} generated from a uniform distribution over [0,20]. The figure shows the output of five neurons taken from each layer. After a short transient, all the neurons in a given layer have approximately

class of models. For instance, while higher order models can be expected to behave qualitatively in a similar way, spiking neuron models ("integrate and fire") may behave differently. Another possibility, is the study of chaos. It has been suggested several times that neural activity has an essential chaotic component. However, very little is known about chaos in systems satisfying (1) or (2).

Finally, there is the issue of how delays can play useful roles in neural computations. For instance, with the help of delays, one could construct a bank of similar oscillators, but with different frequencies within a relatively broad spectrum. These could in turn be used for the analysis or synthesis of general functions or trajectories, using a Fourier type of decomposition, but with bounded frequencies (Baldi (1994)). In a different direction, as already pointed out, delays can vary in an organism over slow time scales, for instance during its growth. As in the case of synaptic weights (von der Malsburg (1981)), one can wonder whether there could exist much faster mechanisms for the adjustment of delays, on a time scale for instance of 100 ms, coupled with the dynamics of the networks themselves. Quickly modifiable delays could help both in the rapid phase-locking and desynchronization of neuronal assemblies, as required in some of the recent theories on binding and attention.

and T is a parameter used to discretize the possible delays. It is clear that in this approach which uses fixed heuristically derived delays, the delays could easily be rendered adjustable by allowing both the width σ and the center $t_i = iT$ of the delay kernel to vary. Both parameters could be adjusted by gradient descent since it is easy, from (36) and (37), to get $\partial o_i/\partial \sigma$ or $\partial o_i/\partial t_i$. Delays could adjust on a slow time scale, for instance across several speakers during the basic development of a speech recognizer, or on a fast time scale to adapt in real time to one particular speaker during normal functioning.

§6 Conclusion

In summary, the introduction of delays in neural networks models such as (1), has a dramatic influence on the stability property of the corresponding networks, as already pointed out by Marcus and Westervelt (1989). In particular, many convergent networks, including symmetric and antisymmetric can become oscillatory as a result of delayed interactions. This enlarges the class of architectures capable of supporting stable oscillations to include, for instance, the case of two reciprocally connected populations of neurons, one exhitatory and one inhibitory. Within oscillatory architectures, the effects of delays seem to be mainly quantitative, such as shifts in the bifurcation points. The most pervasive effect, as can be expected, is a general lowering of the frequency of the oscillations together with a significant broadening of their spectrum and, possibly, a lengthening of the transients. Synchronization effects are not qualitatively altered. Adjustable delays are an additional mechanism through which networks could achieve a broader range of dynamical trajectories. Gradient descent learning equations can be derived accordingly, as well as other possible learning schemes.

There are several possible directions for further investigation. Obviously, one could try to incorporate more biological realism into the models. For example, in the case of the results of Gray et al. (1989) on the first cortical visual areas, one could introduce different cell subpopulations together with a rough columnar organization and short and long range connections with different delays. A different issue is the generality of the results we have derived. Should one expect to observe different phenomena if different model neurons are used? The answer may depend on the

instabilities as a result of bifurcations in the dynamical system. Of course, all these problems remain in the case of recurrent networks with delays, regardless of whether the delays themselves are adjustable or not.

It should be noticed that the learning equations (34) and (36) have been derived without any particular assumption for the function F (other than continuous differentiability). Therefore they can be applied to numerous other models. In particular, they can be used for the alternative form of the additive model given by

$$\frac{du_i}{dt} = -\frac{u_i}{\tau_i} + f_i(\sum_j T_{ij}\, u_j) + I_i \tag{37}$$

and, by discretization of (35) with $\Delta t = \tau_i = 1$, to the usual equations used in connectionist architectures of the type $u_i(t+\Delta t) = f_i(\sum_j T_{ij}\, u_j(t))$, with or without delays. (32) and (34) can also be applied to higher order models with, for instance, interactions terms of the form $T_{ijk}\, u_j\, u_k$.

It is natural to speculate about the possible uses of adaptive delays in neural systems. Especially if implemented on a computer, the algorithm described here, or any of its variations, is not meant to be used for undiscriminate learning of different delays throughout large amorphous and densely interconnected networks with random initial conditions, but rather for the fine tuning of a selected set of parameters in architectures already endowed of a certain degree of structure. In this regard, it is remarkable that in the best studied examples of useful delays, both in natural (Carr and Konishi (1988)) and artificial (Unnikrishnan et al. (1991)) neural systems, the delays are arranged in orderly arrays of delay lines. These delays lines are essentially part of a feedforward network for which the learning task is much more simple. In these examples, different delays are used in order to bring together the effects of temporally separated events onto a coincidence detector type of neuron. For example, in Unnikrishnan et al. (1991), the successive parts of a spoken word are delayed differentially in order to arrive simultaneously onto a unit assigned to the recognition of that particular word. This can be viewed as a "time warping" technique for optimal matching. For a given input $I(t)$, the output of the i-th delay line is given by the convolution

$$o_i(t) = \int_0^{+\infty} K(i,t')I(t-t')dt' \tag{38}$$

where $K(i,t')$ is a gaussian delay kernel

$$K(i,t') = \frac{1}{\sqrt{2\pi}\sigma} e^{-(t'-iT)^2/2\sigma^2} \tag{39}$$

need to be slightly modified to take the delays into account and then, in the case where the delays themselves are learnable, new sensitivity equations need to be added for the adjustement of the delays. For parameters other than the delays, by differentiating (32) and using (2), we have

$$\frac{dp_{iw}(t)}{dt} = -\frac{1}{\tau_i}p_{iw}(t) + \sum_j T_{ij} f_j'(u_j(t-\tau_{ij}))p_{jw}(t-\tau_{ij}) + \frac{\partial F_i}{\partial w} \tag{33}$$

where $\partial F_i/\partial w$ is the explicit derivative of F_i with respect to w, i.e. $\partial F_i/\partial T_{jk} = \delta_{ij} f_k(u_k(t-\tau_{ik}))$, where δ_{ij} is the Kronecker δ. In vector notation

$$\frac{dp_{.w}(t)}{dt} = L(t)p_{.w}(t) + L(t-\tau)p_{.w}(t-\tau) + \frac{\partial F}{\partial w} \tag{34}$$

where $L_{ij}(t) = \partial F_i/\partial u_j(t) = -\delta_{ij}/\tau_i$, $L_{ij}(t-\tau) = \partial F_i/\partial u_j(t-\tau_{ij})$, and $p_{.w}(t-\tau)$ is the vector of components $p_{jw}(t-\tau_{.j})$. When the delays are learnable, we must add for each delay τ a new equation

$$\frac{dp_{i\tau}(t)}{dt} = -\frac{1}{\tau_i}p_{i\tau}(t) + \sum_j T_{ij} f_j'(u_j(t-\tau_{ij}))p_{j\tau}(t-\tau_{ij}) + \frac{\partial F_i}{\partial \tau} \tag{35}$$

where, as usual, $\partial F_i/\partial \tau$ denotes the explicit derivative, i.e. $\partial F_i/\partial \tau_{jk} = -\delta_{ij} T_{ik} f'(u_k(t-\tau_{ik}))du_k(t-\tau_{ik})/dt = -\delta_{ij} w_{ik} f'(u_k(t-\tau_{ik}))F_k(t-\tau_{ik})$. In vector notation

$$\frac{dp_{.\tau}(t)}{dt} = L(t)p_{.\tau}(t) + L(t-\tau)p_{.\tau}(t-\tau) + \frac{\partial F}{\partial \tau} \tag{36}$$

where $p_{.\tau}(t-\tau)$ is the vector of components $p_{j\tau}(t-\tau_{.j})$. To evolve the dynamics forward over the interval $[t_0, t_1]$, the initial conditions on any $u_i(t)$ must be defined over the interval $[t_0 - \alpha_i, t_0]$ where $\alpha_i = \max_j \tau_{ji}$. If, as it is often the case, these conditions are chosen independently of the relevant parameters, then $p_{iw}(t) = 0$ for $t_0 - \alpha_i \leq t \leq t_0$. In any case, once these initial conditions are determined, the sensitivity equations (33) and possibly (35) can be evolved forward in time, as for example in Williams and Zipser (1989) for the case of synaptic weight parameters, although this is computationally expensive. As in the case of weight parameters in systems without delays, alternatives approaches can be used, such as random direction descent, back-propagation through time for delays or, equivalently, adjoint methods for delayed differential equations (see Hale (1977), (Atiya and Parlos (1992), Baldi (1993)). Gradient descent learning of weight parameters in recurrent networks can encounter several problems. For instance, the learning procedure can encounter

Here, we shall concentrate on one possible algorithm for adjusting the weights by gradient descent. Our purpose is to briefly see how delays affect the usual back-propagation equations for recurrent networks (see, for instance, Pineda (1987), Pearlmutter (1989) and Williams and Zipser (1989)) and how delays can be tuned incrementally to achieve optimal performance. Thus, we assume that the overall performance of a network can be measured by an error function $\mathbf{E}$. Any adjustable parameter w is modified so as to reduce $\mathbf{E}$ by gradient descent

$$\frac{dw}{dt} = -\eta \frac{\partial \mathbf{E}}{\partial w} \tag{28}$$

where η is the usual learning rate, or the relaxation time constant of the parameter dynamics. In the case of fixed point learning, delays have no effect on the gradient descent learning equations. This is because all the relevant expressions are computed at equilibrium, when the vector du/dt is constantly 0. Of course they affect the activation dynamics and can change the fixed point associated with a given initial state, thus still influencing the learning dynamics in an undirect way.

In the more general case of trajectory learning, the goal is to modify the parameters so that u follows a prescribed trajectory u^* over a time interval $[t_0, t_1]$. The error function is of the form

$$\mathbf{E} = \int_{t_0}^{t_1} E(u, u^*, t) dt \tag{29}$$

where $E(u, u^*, t)$ is the instantaneous error. For instance, in the usual LMS case

$$\mathbf{E} = \int_{t_0}^{t_1} (u^*(t) - u(t))^2 dt = \int_{t_0}^{t_1} \sum_i (u_i^*(t) - u_i(t))^2 dt \tag{30}$$

computed over the visible units and possibly over the sub-time intervals at which $u^*(t)$ is defined. To update the weights, we need to compute the gradient

$$\frac{\partial \mathbf{E}}{\partial w} = \int_{t_0}^{t_1} \sum_i \frac{\partial E}{\partial u_i} \frac{\partial u_i}{\partial w} dt = \int_{t_0}^{t_1} \Big(\frac{\partial E}{\partial u}\Big)^t \frac{\partial u}{\partial w} dt = \int_{t_0}^{t_1} \Big(\frac{\partial E}{\partial u}\Big)^t p_{\cdot w} \, dt \tag{31}$$

($\partial E / \partial u_i = 2(u_i(t) - u_i^*(t))$ for visible units and 0 otherwise) where the coordinates

$$p_{iw}(t) = \frac{\partial u_i(t)}{\partial w} \tag{32}$$

of the sensitivity vector $p_{\cdot w}(t)$ represent how the coordinates u_i at time t vary with a small change in w. Now, the equations for the sensitivities of the usual parameters

neocortex, the two layer structure of reciprocally connected excitatory and inhibitory neurons is ubiquitous, and so is also the presence of delays. Delays, however, are not the unique ingredient for oscillatory behavior since a high degree of cortical intralayer connectivity is also present.

As in our previous study, simulations show that as connections become more local or as connections within each layer are added, the zero phase-locking of cells within a layer can degrade in a smooth fashion. The case of intralayer connectivity can again be taken into account by averaging, and studying the behavior of ring networks with additional self connections. In the case of lateral inhibition, often seen in biological networks, the analysis of small oscillations beyond the bifurcation point is essentially as in the previous section. This is because the self-connection term, when linearized, can be combined with the decay term $-u_i/\tau_i$.

Finally, we have seen here that intralayer zero-phase-locking can result from the convergence and divergence of the pattern of connections over long ranges. As in (Atiya and Baldi (1989)), zero-phase-locking in two independent but statistically similar layered networks of units satisfying (3) can also be achieved by the administration of a common pulse of sufficient energy to all the cells of two corresponding layers simultaneously. The synchronizing signal could be interpreted, for instance, in terms of a common feedback message arriving on the two networks (Gray et al. (1989)).

§4 Learning with Delayed Interactions

In this section, we examine the effects of delays on the adaptation properties of neural networks. The influence of delays on learning algorithms can be twofold. First, they affect the learning of other parameters such as gains, time constants or synaptic weights. Second, delays themselves may be part of the adjustable parameters of a neural system so as to increase the range of its dynamical capabilities. Although there is no conclusive evidence for continuously adjustable delays in biology, there exist numerous examples of finely tuned delays and delay lines and certainly many delays are subject to variations, for instance during the growth of an organism. For sure, several possible biophysical mechanisms can be envisioned by which adjustable delays could be achieved.

this approach. Their main result is entirely consistent with this work and consist, as can be expected, in a significant depression of the overall frequency of the system.

Here, as in our previous paper, we shall consider one specific application of the results on ring networks to a particular class of biologically motivated architectures consisting of laminated networks, i.e. networks where neurons are partitioned into several interconnected layers, each layer being relatively homogeneous, at least on a large scale. This class of architectures is common in nervous tissue, for instance in the cortex or the olfactory bulb. The models considered here, however, are extremely simplistic and not geared towards the detailed modeling of any particular body of neurophysiological data. Instead, we would like to show how the results on rings can be applied to shed some light on the limit cycles and synchronization properties of layered networks, and corroborate our results with numerical simulations. It should also be noticed that the model units located in two different layers could also be intended to represent two distinct subpopulations of neurons, physically located in the same layer.

To begin with, we assume that all the connections occur between one layer and the next in a cylic fashion (fig. 4b). Each unit in each layer projects to all the units in the following layer but no connections exist between units pertaining to the same layer. The sign of the projections of all the units of a given layer is constant, i.e. within a layer all the units are either excitatory or inhibitory. Simulations of such networks with and without delays, show that when there is sufficient uniformity among the parameters characterizing the populations of units of each layer, then all the neurons pertaining to the same layer behave essentially in exactly the same way. Moreover, this behavior can be approximated with great accuracy by first replacing each layer by one average unit whose properties are the average of the properties of the corresponding population, and then looking at the behavior of the corresponding ring using the results in the previous section. A detailed example is given in fig. 5. In particular, if the number of inhibitory layers is odd and if all the gains (and/or weights) are beyond a certain bifurcation value, then the network rapidly converges to a stable limit cycle where all the units within one layer are zero-phase-locked, and where a constant phase shift exists between any two consecutive layers. Thus, in this respect, the situation is very similar to the case where ther are no delays (Atiya and Baldi (1989)), except of course that the bifurcation point is shifted, and the overall period is larger, as a result of delays. One notable difference, as can be expected from the previous section, is that a *two* layers system, with one excitatory and one inhibitory layer, can oscillate when delays are present. In olfactory cortex and

As can be observed in fig. 3, the formula obtained for the period, near the bifurcation point and in the high gain limit, are very accurate. Between these two regimes, from simulations the period appears to be an increasing function of the delays. From (9), we see also that, as we increase the delays and thus decrease w, the amplitude also tends to increase. As a result, especially when delays are present, (21) has in fact a wide range of applicability. Usually the period scales like the sum of the time constants and the delays, so that w is small with respect to τ_i. Therefore, if we take the first order approximation to the trascendental functions in (19) and (21) we get immediately

$$\frac{\pi}{\sum_i \tau_{ii-1} + \sum_i \tau_i} \leq w \leq \frac{\pi}{\sum_i \tau_{ii-1} + \ln 2 \sum_i \tau_i} \tag{27}$$

which yields (23). Thus, without delays, the range of achievable periods is given by $(2 - 2\ln 2)\sum_i \tau_i$. With delays satisfying $0 \leq \tau_{ii-1} \leq \tau_i$, the range becomes $(4 - 2\ln 2)\sum_i \tau_i$, with a 3.5 fold increase. Within the topic of oscillations, this is the most striking effect of delays. This effect points to the obvious advantages that could result from having adjustable delays. As can be expected from the results on the limit cycles, we also observe, in simulations, that delays can increase the duration of the transients.

§4 Layered Networks and Synchronizations

Ring networks are of limited biological relevance. However, they can be regarded as building blocks for more realistic architectures. Indeed, to study the behavior of more complex networks, one possible approach is to decompose them into rings and apply the results of the previous section for each one of them. When the rings are operating in their oscillatory mode, the problem reduces to the study of large networks of coupled oscillators. When there is some degree of uniformity in the individual oscillators and in the pattern of couplings, such as a lattice or a fully interconnected system, then one may be able to draw some conclusions using the coupled limit cycle aproach, i.e. by representing each oscillator by one parameter: its phase along its cycle (see, for instance, Sakaguchi et al. (1987), Kopell and Ermentrout (1988), Baldi and Meir (1990), and references therein). The effects of delays in a two dimensional lattice of coupled oscillators have been studied by Niebur et al. (1991) directly using

In general, to a first approximation the period $2\pi/w$ of the limit cycle satisfies

$$2(\sum_i \tau_{ii-1} + \ln 2 \sum_i \tau_i) \leq \frac{2\pi}{w} \leq 2(\sum \tau_{ii-1} + \sum_i \tau_i) \tag{23}$$

In particular, a ring with delays in the range $0 \leq \tau_{ii-1} \leq \tau_i$ can achieve a range of limit cycle periods which is roughly 3.5 times the range achievable by the corresponding network without delays.

Proof: From (15),

$$[(x + \frac{1}{\tau})^2 + y^2]^{n/2} = -GTe^{-sx} \tag{24}$$

and

$$n \arctan \frac{\tau y}{\tau x + 1} = \pi - sy \tag{25}$$

It is then easy to see that, if $GT\tau^n < 1$, then $x < 0$ and the origin is stable. At a Hopf bifurcation, we must have $x = 0$ and $y \neq 0$ (see Hale (1979) for a treatment of Hopf bifurcations in delayed systems). Therefore, we must have

$$(\frac{1}{\tau} + iy) = (G|T|)^{1/n} e^{-i(sy-(2k-1)\pi)/n} \tag{26}$$

$k = 0, ..., n-1$ from which $y = \pm\sqrt{\tau^2(G|T|)^{2/n} - 1}/\tau$. It is easy to see that if y is a solution of (26), so is $-y$. Therefore we can assume that $y > 0$ ($y = 0$ is not a solution by direct inspection). As the product $G|T|$ increases, y increases too. Therefore, for the first bifurcation, we want to find the smallest y satisfying (26). By continuity of both hand sides in (26), it can be seen that the smallest solution y is such that $0 < y < \pi/s$ with $k = 0$. In which case, from the real part of (26), we find that at the first bifurcation point the various parameters must satisfy (18). The other results on the eigenvalues follow easily from (24) and (25). (19) (resp. (21)) results from adding the delays of (10) (resp. (12)) once around the loop. (20) (resp. (22)) is a direct application of (10).

It can easily be seen that in the case of a two ring with one excitatory and one inhibitory connection (not necessarily antisymmetric) and delay $s > 0$, the bifurcation equation (18) has always a solution c satisfying $1/\tau^2 < c < 1/\tau^2 + \pi^2/s$. Therefore, for any delay $s > 0$, no matter how small, one can find a value for the gains so that the corresponding ring is oscillatory. This, as already pointed out, is in sharp contrast with the case $n = 2$ and $s = 0$ which does not lead to oscillations (unless self-connections are also added).

It is then easy to see that, if $GT\tau^n < 1$, then $x < 0$. If $GT\tau^n = 1$, then $x = 0$ implies $y = 0$ so that the bifurcation occurs when the rightmost eigenvalue is the origin. The rest follows similarly from (16) and (17). It should be noticed that here, as in the next case, a general geometric lower bound on the period of periodic solutions can be derived using the results in Busenberg et al. (1986 and 1987). The lower bound is $6/L$ where L is the Lipschitz constant of the differential system. For instance, for a ring with $g_i = g$, $\tau_i = \tau$ and $T_{ii-1} = \pm T$, the Lipschitz constant is at most $gT + 1/\tau$. Better estimates for the period of stable limit cycles will be derived below.

2nd case: odd number of inhibitory connections (T < 0). The origin is always the only fixed point. Let us assume, for simplicity, that $\tau_i = \tau$. Then a Hopf bifurcation occurs when the product of the magnitudes of the gains and the weights satisfies $G|T| = c$ where

$$c^{1/n} \cos\Big(\frac{\tau\pi - s\sqrt{\tau^2 c^{2/n} - 1}}{n\tau} \Big) = \frac{1}{\tau} \tag{18}$$

When $G|T| < c$, and in particular when $G|T|\tau^n < 1$, then the origin is stable. When $GT > c$, the origin is unstable. When the origin is unstable, the network always rapidly converges to a stable limit cycle (see fig. 2). When n is even, there are no real eigenvalues. When n is odd, there are 0,1 or 2 real eigenvalues which are necessarily negative. Near the bifurcation, the amplitude, period and phase shifts of the quasi sinusoidal oscillations can be approximated by linearization. This yields

$$w \sum_i \tau_{ii-1} + \sum_i (\arctan \tau_i w) = \pi \tag{19}$$

If β_i is the relative delay shift of the oscillation of u_i with respect to u_{i-1}, then

$$\beta_i = \begin{cases} -\tau_{ii-1} - (\arctan \tau_i w)/w & \text{if } T_{ii-1} > 0 \\ -\tau_{ii-1} + (\pi - \arctan \tau_i w)/w & \text{if } T_{ii-1} < 0 \end{cases} \tag{20}$$

In the high gain limit, the units rapidly converge to a square wave oscillation, i.e $V_i(t) \approx \text{sign}(\sin w(t + \phi))$. In this regime, the period can be approximated from the relation

$$w \sum_i \tau_{ii-1} + w \sum_i \tau_i \ln(2/1 + e^{-\pi/w\tau_i}) = \pi \tag{21}$$

If β_i is the phase shift of the oscillation of u_i with respect to u_{i-1}, then

$$\beta_i = \begin{cases} -\tau_{ii-1} - \tau_i \ln(2/1 + e^{-\pi/w\tau_i}) & T_{ii-1} > 0 \\ \pi/w - \tau_{ii-1} - \tau_i \ln(2/1 + e^{-\pi/w\tau_i}) & T_{ii-1} < 0 \end{cases} \tag{22}$$

If the ring oscillates in one of these two regimes, then by adding up all the phase shifts (10) or (12) once around the ring one must find a multiple of the period. This type of relation will be exploited below.

The characteristic equation of (6) is

$$\det(M + e^{-\lambda s} N - \lambda I) = 0 \tag{13}$$

which yields, after expanding the determinant,

$$\prod_{i=1}^{n} (\lambda + \frac{1}{\tau_i}) = e^{-\lambda s} GT \tag{14}$$

with $T = \prod_1^n T_{ii-1}$ and $G = \prod_1^n g_i$. In what follows we shall need also $\Gamma = \prod_1^n \tau_i$. When $\tau_i = \tau$, letting $\lambda = x + iy$, (14) becomes

$$(x + \frac{1}{\tau} + iy)^n = GTe^{-sx} e^{-isy} \tag{15}$$

As in the case of (3) without delays, two cases need to be distinguished.

1st case: even number of inhibitory connections (T > 0). If $GT\Gamma \leq 1$, then the origin is the only fixed point. If $GT\Gamma > 1$, then in addition to the origin there are two symmetric fixed points. Let us assume, for simplicity, that $\tau_i = \tau$. Then if $GT\tau^n < 1$, all eigenvalues have negative real parts and the origin is stable. A pitchfork bifurcation occurs when $GT\tau^n = 1$, through a $\lambda = 0$ eigenvalue. When $GT\tau^n > 1$ the origin is unstable. If n is odd, there is only one real eigenvalue solution of (14) which is positive if and only if $GT\tau^n > 1$. If n is even, there is 1,2 or 3 real eigenvalues, only one of which is positive whenever $GT\tau^n > 1$. Simulations show that there are no stable limit cycles and the network in general converges to one of the two symmetric fixed points. There are, however, unstable periodic solutions. From simulations, for a fixed set of parameter values, the degree of instability of these periodic solutions seems to decrease as n increases (see fig. 1).

Proof: The determination of the fixed points is exactly the same as in the case without delays treated in Atiya and Baldi (1989). From (15),

$$[(x + \frac{1}{\tau})^2 + y^2]^{n/2} = GTe^{-sx} \tag{16}$$

and

$$n \arctan \frac{\tau y}{\tau x + 1} = -sy \tag{17}$$

the origin, is given by

$$\begin{cases} dv_1/dt = -v_1/\tau_1 + T_{1n}\, g_n\, v_n(t-s) \\ dv_2/dt = -v_2/\tau_2 + T_{21} g_1 v_1(t) \\ \cdots \\ dv_n/dt = -v_n/\tau_n + T_{nn-1} g_{n-1} v_{n-1}(t) \end{cases} \tag{5}$$

or, in matrix form,

$$\frac{dv}{dt} = M\, v(t) + N\, v(t-s) \tag{6}$$

where M and N are the obvious matrices defined by (5). As a last preliminary and before we look at the bifurcation of (5) as the parameters are varied, it is useful to look at the behavior of a single unit in the ring under a steady oscillatory input, sinusoidal in the case of small oscillations and square wave in the high gain limit. In the case of small sinusoidal input with amplitude $A > 0$, period $2\pi/w$ and delay α, the charging equation of a unit can be linearized in the form

$$\frac{du}{dt} = -\frac{u}{\tau} + ATg \sin w(t-\alpha) \tag{7}$$

The solution to (7) is

$$u(t) = B \sin w(t+\beta) + Ce^{-t/\tau} \tag{8}$$

where the positive amplitude B is given by

$$B = -\frac{ATg}{w} \sin w(\alpha+\beta) = \frac{A|T|g\tau}{\sqrt{1+\tau^2 w^2}} \tag{9}$$

and the delay shift β by

$$\beta = \begin{cases} -\alpha - (\arctan \tau w)/w & \text{if } T > 0 \\ -\alpha + (\pi - \arctan \tau w)/w & \text{if } T < 0 \end{cases} \tag{10}$$

(the constant C is irrelevant for most purposes). In the high gain limit with square wave oscillations and delay α, the charging equation of a unit becomes

$$\frac{du}{dt} = -\frac{u}{\tau} + T\text{sign}(\sin w(t-\alpha)) \tag{11}$$

It is easy to see that this equation has a high gain solution $V = \text{sign}\, u = \text{sign}(\sin w(t+\beta))$ if and only if the phase shift β satisfies

$$\beta = \begin{cases} -\alpha - \tau \ln(2/1 + e^{-\pi/w\tau}) & T > 0 \\ \pi/w - \alpha - \tau \ln(2/1 + e^{-\pi/w\tau}) & T < 0 \end{cases} \tag{12}$$

§3 Oscillator Rings

Although there exist examples in biology of single neurons with intrinsic oscillatory properties, collective neural oscillations are believed to result to a great extent from network properties. Thus, as in our previous work, we begin by looking at the most simple class of architectures capable of sustained oscillations, and that consists of a ring of neurons connected cyclically (fig.4 a). With delayed interactions, this leads to the system

$$\frac{du_i}{dt} = -\frac{u_i}{\tau_i} + T_{ii-1} f_{i-1}(u_{i-1}(t-\tau_{ii-1})) \tag{3}$$

$i = 1, ..., n$. In the absence of delays, such a cyclic feedback system has stable oscillations if and only if three conditions are met (Atiya and Baldi (1989)). The number of inhibitory connections must be odd as expected from Hirsch's result, the gains g_i of the transfer functions f_i (and/or the magnitude of the weights) must be large enough beyond a Hopf bifurcation point, and $n \geq 3$. As we shall see, when delays are present, the situation for (3) is very similar with one notable exception. As can be expected from the discussion in the introduction, the first two conditions remain true. However, when delays are present, a two-neuron loop can also have a stable oscillatory regime. In Van der Heide (1980), it is shown that in the special case of $n = 2$ and $T_{12} = -T_{21} = 1/\tau_1 = 1/\tau_2$, if the product $g_1 g_2$ of the gains exceeds a certain lower bound, then (3) has a non constant periodic solution with a period larger than $2(\tau_1 + \tau_2)$ and this even in the case of arbitrarily small delays. This provides also an example of an oscillatory antisymmetric network.

One first important remark on (3), is that this system can be reduced to a system with only one delay. Indeed, if we let $v_i(t) = u_i(t - \sum_{j=i+1}^{n} \tau_{jj-1})$ for $i = 1, ..., n-1$ and $v_n(t) = u_n(t)$, we obtain a new equivalent system with only one delay $s > 0$, equal to the sum of all the previous delays $s = \sum_i \tau_{ii-1}$, defined by

$$\begin{cases} dv_1/dt = -v_1/\tau_1 + T_{1n} f_n(v_n(t-s)) \\ dv_2/dt = -v_2/\tau_2 + T_{21} f_1(v_1(t)) \\ \dots \\ dv_n/dt = -v_n/\tau_n + T_{nn-1} f_{n-1}(v_{n-1}(t)) \end{cases} \tag{4}$$

The fixed points of (3) coincide with the fixed points of the same system without delays. In particular, the origin is a fixed point. The linearized version of (4), around

When the connection matrix $\mathbf{T} = (T_{ij})$ is symmetric, it is well known that the dynamics of (1) is always a convergent gradient dynamics. This has been the basis for applications of models such as (1) to associative memory and optimization problems. However, when $\mathbf{T}$ is symmetric and provided the gains are sufficiently high, (2) is not necessarily convergent, and this *even if the delays* τ_{ij} *are symmetric*. In particular, even it the delays are all the same ($\tau_{ij} = \tau$) across the network, the dynamics of (2) is still not convergent as shown by Marcus and Westervelt (1989). In fact, these authors have conducted an extensive analysis of the effects of one common delay on the stability of (2), especially as a function of network architecture. Our approach, however, is different in two important respects: first we want to allow for different possible delay values across the network and, second, we are interested in dynamics and specifically on oscillations rather than fixed point stability. As a result, we do not view the absence of convergence as something negative which needs to be avoided, but rather as an essential ingredient of neural computations. Another class of stable networks in the absence of delays correponds to the case of antisymmetric connections, i.e. $T_{ij} = -T_{ji}$ and $T_{ii} = 0$ (Atiya and Baldi (1989)) with $I = 0$. As we shall see in the next section, antisymmetric networks become unstable in the presence of delays.

There exists a different result on the convergence of systems satisfying (1) which is of relevance here since it applies also to (2). Hirsch (1987) has shown that, under some assumptions *, if in the graph of connections of (1) every loop contains an even number of inhibitory connections, then the corresponding network is almost quasiconvergent. In particular, it does not have any stable limit cycles. The absence of loops with an odd number of inhibitory connections reflects an absence of frustration in the corresponding physical system. The proof of this result is done by using the even loop property, and changing the sign of some of the variables, to reduce the problem to the case of a cooperative system with only positive interactions, that therefore cannot oscillate. In the case of (2), the same reduction leads to a cooperative system with delayed interactions which is also convergent (Smith (1987)). Finally, for completeness, it must also be noted that for some differential systems, delays may in fact lead to increased stability (see Hale (1979) for examples). However, we did not encounter, nor tried to construct, such an example satisfying a system of the form of (2).

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* The key assumption, in the case of neural networks, is that the Jacobian of the differential system be irreducible. In neural terms, this requires that the output of every neuron be able to influence the activity of any other neuron in the network, even if through an indirect pathway.

we shall assume, that only one past synaptic event per synaptic interaction is needed. Thus, in what follows, the network dynamics is described by

$$\frac{du_i}{dt} = F_i = -\frac{u_i}{\tau_i} + \sum_j T_{ij} f_j(u_j(t-\tau_{ij})) + I_i \qquad (2)$$

and the purpose is to understand how the delays τ_{ij} affect the behavior of (2) with respect to (1). More general convolution models for delays are possible (see, for instance, de Vries and Principe (1991)) by introducing a time dependent interaction matrix and then writing the interaction term in (2) as $\sum_j \int_0^t T_{ij}(s) f_j(u_j(t-s)ds$. Little can be said, however, in this general setting, and in most applications one is forced to revert to some form of discretized delays.

We begin, in the next section, by briefly reviewing how delays disrupt the convergence properties of (1). In the following sections, 3 and 4, we study the effects of delays on oscillatory properties. Oscillations in (1) have been investigated in Atiya and Baldi (1989). Here, we extend their results to (2) by following a similar strategy. Since oscillations cannot arise without feedback, we first examine in section 3 the most simple oscillatory network consisting of a ring of neurons. Analytical results are derived, by linearization and in the high gain limit, and shown to be in excellent agreement with numerical simulations. The results are then applied in section 4 to more complex and more biologically motivated networks. Finally, in section 5, we examine how delays can affect learning, and consider the issue of adaptable delays and derive a corresponding gradient descent learning algorithm.

§2 Effects on Convergence

As already pointed out, one important effect of delays regards stability and especially convergence properties. When delays are introduced in (1), many networks lose their convergence, with some trivial exceptions such as feedforward networks or networks with very small gains and/or synaptic weights. For instance, even in the case of one unit connected to itself which is obviously convergent in the absence of delays, oscillations can arise as soon as delays are present (Hadeler and Tomiuk (1977)). Two additional classes of networks which loose their convergence properties with the introduction of delays are symmetric and antisymmetric networks.

§1 Introduction

Integration and communication delays are ubiquitous, both in biological and man-made neural systems. It is therefore natural to ask what effects these delays have on the dynamics and other properties of neural networks. In addition, delays are often considered as a nuisance by circuit designers, and for at least two reasons: they slow down the rate at which information is processed, and they often tend to introduce some degree of instability in the circuits. Yet, a mounting body of evidence, especially from neurobiology, seems to indicate that delays, especially if adaptive, can in fact be useful (see, for instance, Carr and Konishi (1988) and Lisberger and Sejnowski (1991), Unnikrishnan et al. (1991)). Indeed, delays should be considered as an additional media through which evolution, or skilled engineers, can achieve particular dynamical effects. In particular, in connection with several findings in the last few years (Gray and Singer (1989)), regarding the distant synchronization of fast gamma (35-80 Hz) oscillations in the brain, and their possible hypothetical contribution to feature binding and other cognitive effects (von der Malsburg (1981), Baldi and Atiya (1989), Sompolinsky et al. (1990), Crick and Koch (1990), Wilson and Bower (1991)), we are interested in the effects of delays on oscillatory behavior in general and, more specifically, on the phase-locking of distant populations of coupled oscillators.

Here, we propose to study the effects of delays on neural dynamics by using the usual additive neural network model (see, for instance, Hopfield (1984)) which is a one-compartment model for each neuron. Accordingly, the internal membrane potentials u_i are governed by

$$\frac{du_i}{dt} = -\frac{u_i}{\tau_i} + \sum_j T_{ij} f_j(u_j) + I_i \tag{1}$$

$i = 1, ..., n$. T_{ij} are synaptic connection strengths, τ_i time constants, I_i external inputs and f_i input-output transfer functions, usually sigmoids with gain g_i. To fix the ideas, in what follows we shall use $V_i = f_i(u) = \tanh(g_i u)$ but the results remain true for any odd function f which is concave down for $u > 0$. Time delays can easily be introduced in the previous model by writing the interaction term in the form $\sum_j \sum_P T_{ijP} f_j(u_j(t - \tau_{ijP})$, where P is an index which refers to past synaptic events and $\tau_{ijP} \geq 0$. In general, the current state of a synapse may depend on several events having occurred in the neighboring neurons at different times. Here, for simplicity,

SUMMARY

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3. Oscillator Rings

4. Layered Networks and Synchronizations

5. Learning with Delayed Interactions

6. Conclusion

Figure Captions
Acknowledgements
References

How Delays Affect Neural Dynamics and Learning

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Abstract: We investigate the effects of delays on the dynamics and, in particular, on the oscillatory properties of simple neural network models. We extend previously known results regarding the effects of delays on stability and convergence properties. We treat in detail the case of ring networks for which we derive simple conditions for oscillating behavior and several formulas to predict the regions of bifurcation, the periods of the limit cycles and the phases of the different neurons. These results in turn can readily be applied to more complex and more biologically motivated architectures, such as layered networks. In general, the main result is that delays tend to increase the period of oscillations and broaden the spectrum of possible frequencies, in a quantifiable way. Simulations show that the theoretically predicted values are in excellent agreement with the numerically observed behavior. Adaptable delays are then proposed as one additional mechanism through which neural systems could taylor their own dynamics. Accordingly, we derive recurrent back-propagation learning formulas for the adjustment of delays and other parameters in networks with delayed interactions and discuss some possible applications.

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